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Vibratory communication in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae)

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Vibratory communication in the wolf spider *Hygrolycosa rubrofasciata* **(Araneae, Lycosidae).** - The male of the European species *Hygrolycosa rubrofasciata* (Ohlert) produces percussive sounds that are audible to a human ear from a distance of several metres. The acoustic effect is generated by rapidly tapping the abdomen against the substrate (often dry leaf litter). The proximity of a female or female draglines does not seem necessary for inducing this 'calling' behaviour. The resulting drumrolls are elicited at intervals by the rambling male. The duration of a pulse-train in a 'calling' drumroll is about 1 s, and period length between pulse peaks c. 30-40 ms. A receptive female close to the male will respond by oscillating her abdomen, producing a percussive sound considerably weaker and more variable in duration than the male's 'calling' drumroll. Reciprocal drumming will take place in alternation until the sexes meet for copulation. Percussive male-female 'duetting' is sofar not known from any other lycosid species. In male-male encounters, a dominant male will exhibit a specific agonistic behaviour which includes series of brief drumrolls produced by abdominal tapping. The male's ability to perform abdominal percussion is morphologically concomitant with the venter of his abdomen being covered by knob-like hairs. Specific cuticular structures at the male's tibio-cymbial joint are arranged as to form a stridulatory apparatus (no stridulatory sound or vibration has as yet been discerned). A similar condition in male *Hygrolycosa umidicola* Tanaka (from Japan) indicates that this tibio-cymbial configuration is an apomorphic trait at some supraspecific level.

Key-words: Araneae - Lycosidae - *Hygrolycosa* - vibratory communication - sound production - stridulatory apparatus

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INTRODUCTION

Communication by percussion, stridulation, or vibration of body parts is well documented in cursorial spiders (e. g. BARTH 1982, 1993; UETZ & STRATTON 1982). The males of various wolf spider species use one or more of these ways for producing substrate-borne vibrations and/or airborne sounds (for refs. see UETZ & STRATTON 1982). As a vibration source generates both substrate-borne vibrations and sound, it is usually difficult to tell, without further analysing, which portions are of biological significance and which sensory pathways are involved. In this paper, the communication by bodily vibrations in the wolf spider *Hygrolycosa rubrofasciata* (Ohlert) (Fig. 1) is presented as revealed from sound production and as inferred from morphological adaptations. Without doubt, substrate-borne vibrations are generated along with the sound, though no equipment was available to the author for recording these.

Percussive signalling is previously known to occur in *H. rubrofasciata*. The male performs drumming behaviour by rapidly tapping on dry leaves by the abdomen which is ventrally covered with numerous short knob-like hairs [unpublished study by O. von Helversen (referred to in ROVNER 1975, WEYGOLDT 1977, BARTH 1982, and UETZ & STRATTON 1982), KRONESTEDT 1984, KÖHLER & TEMBROCK 1987]. This behaviour is performed by males searching for females and the sound produced during what may be regarded as a 'calling' drumroll. Oscillograms of the sound resulting from such drumrolls are given in WEYGOLDT (1977, from von Helversen), KRONESTEDT (1984) and KÖHLER & TEMBROCK (1987).

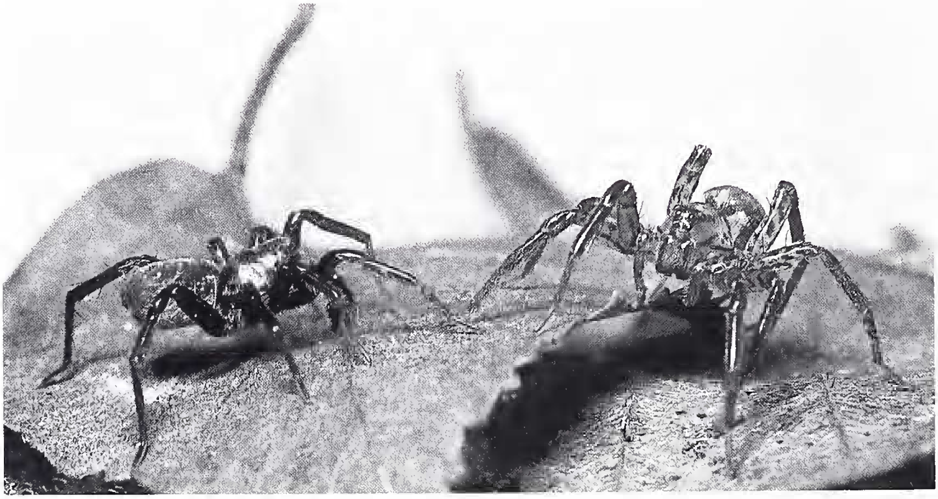

FIG. 1

A pair of *Hygrolycosa rubrofasciata* (the cryptically coloured male to the left) on dry leaves. The species has a body length of 5-7 mm (males usually smaller than females).

As briefly mentioned by KRONESTEDT (1984), a receptive female of *H. rubrofasciata* responds to a calling male by specific percussive behaviour, so far known unique among lycosid spiders. Moreover, a distinct percussive behaviour is exhibited by a dominant male in male-male encounters. In the present paper, this will be further accounted for.

DISTRIBUTION, HABITAT AND PHENOLOGY

The distribution of *Hygrolycosa rubrofasciata* is sofar known restricted to Europe. Currently only two more species are allocated to the same genus (PLATNICK 1993), viz. *H. umidicola* Tanaka, 1978, from Japan, and *H. alpigena* Yu & Song, 1988, from China, the latter in need of further taxonomic evaluation.

BRAUN (1976) summarized literature data on habitat. According to different authors, *H. rubrofasciata* is confined to various wet habitats including certain bogs, fens, wet meadows and swampy forests. KÖHLER & TEMBROCK (1987) found the species on dry, exposed sites with an amount of dry leaves on the ground, adjacent to a swampy *Alnus glutinosa* forest. They assumed that the spiders did move from the swampy forest to adjacent dry sites because of the abundance of dry leaves in the latter. The material for the present study was collected in a swampy forest with *Alnus glutinosa* and *Betula pubescens* growing in groups on small "islets" covered with numerous dry leaves. In April and early May, the ground was more exposed to the sun than later in the season. *Myrica gale*, *Carex elata*, and *Sphagnum* sp. were abundant in the more wet parts of the locality.

BRAUN (op. cit.) also reviewed the phenological information about *H. rubrofasciata*. Various sources indicate that adult males have been found both in spring and autumn. This was confirmed by v. BROEN & MORITZ (1963) who recorded the activity by pitfall traps throughout the season in N-Germany and found a main male activity period in spring to early summer and a slight male activity in autumn. Own collecting by hand as well as by pitfall trapping in the vicinity of Stockholm indicated that adults of a new generation appear in autumn, overwinter and mate during the following spring (KRONESTEDT 1984).

Hygrolycosa rubrofasciata is diurnal. KÖHLER & TEMBROCK (1987) noted that the drumming activity of the males ceases during windy conditions. Moreover, they assumed that higher temperatures promoted drumming behaviour.

MATERIAL AND METHODS

Hygrolycosa rubrofasciata was studied during 1980-83, with some additional observations in 1995. Material was collected in a swampy forest in Täby (c. 10 km N of Stockholm), Sweden. Specimens were taken as adults (females early in spring to ensure their virginity), kept in captivity indoors and observed in a plastic jar (slightly widening from bottom upwards) with or without dry leaves on its bottom. A segment of the jar was cut off and covered by a vertical Plexiglas plate through which observations could be made and photographs taken from a side-view. Sounds were recorded by a UHER 4200 Report tape recorder (microphone UHER M537) from specimens performing on plates of paperboard inserted in the jar at some distance from its bottom. In 1995, some of the recorded sequences were played back into a CSL™ Computerized Speech Lab, model 4300 (Kay Elemetrics Corp) for obtaining oscillograms of the pulse-trains. Lengths of period between pulse peaks were calculated by moving a cursor along enlarged versions of the oscillograms and noting the time values given on the computer screen. For calculating the dispersion of period values (between pulse peaks) in a drumroll, the 20 medial periods were used. The values are given as mean ± SD.

RESULTS

BEHAVIOURS INVOLVED IN VIBRATORY COMMUNICATION

Male 'calling' behaviour

During the mating season, the male exhibits a seemingly rambling seaching behaviour by wandering and halting at intervals. While halting, the male may exhibit a 'calling' behaviour by rapidly tapping the abdomen against the substrate, thus producing a train of pulses here referred to as a 'drumroll' (Figs. 3 & 5). During drumming, the male may remain on the spot or take a few steps. When standing on a dry leaf, the sound resulting from the drumming is amplified by the leaf and may be perceived by a human ear from a distance of several metres. After one or more drumrolls (Figs. 2 & 4), the male may move to another object and repeat the drumming. In the presence of a receptive female close to the male (as among leaves below), a reciprocal 'duet' of percussive signalling will take place. At this instance, the male's searching behaviour turns into courtship display and the 'calling' drumroll may be regarded as a 'courting' drumroll.

TABLE I

Measurements from 5 consecutive 'calling' drumrolls in each of three *Hygrolycosa rubrofasciata* males (c. 21-23°C)

	Duration of one drumroll (median and range in ms)	Number of pulses/drumroll (median and range)	Length of period (in ms) between pulse peaks [mean and SD of pooled 20 medial periods in each drumroll (i. e., N = 100)]
Male 1	1162 (1076-1275)	31 (29-35)	38.6 ± 2.2
Male 2	1479 (1239-1592)	43 (37-44)	35.1 ± 2.3
Male 3	1183 (1148-1234)	34 (33-35)	36.7 ± 1.7

The 'calling' drumrolls have a duration magnitude of around 1 s. The data presented in Table 1 are all between 1 and 1.5 s though considerably shorter drumrolls were recorded at other occasions, e. g. one of c. 720 ms including about 25 pulses, and longer drumrolls during reciprocal intersexual signalling (see below).

As expected, the pulse-rate seems to be temperature-dependent. The following values of period length between pulse peaks were obtained from the same male before and after raising the temperature: at c. 17°C 44.2 ± 2.6 ms (drumroll consisting of 32 pulses) and at c. 25°C 33.8 ± 1.9 ms (33 pulses).

Shortly before and during the emittance of a 'calling' drumroll, the male will perform oscillations of the palps, the tips of which are in contact with the substrate (though they may slip). An indistinct sound of slightly increasing strength can be heard together with a weak humming sound just prior to a 'calling' drumroll which in turn is followed by a rattling sound at the end. It is presently not known whether any sound can be attributed specifically to the palpal oscillations.

Female 'replying' behaviour and male-female percussive 'duetting'

A receptive female will respond to a male's signalling by rapidly oscillating her body. A sound is generated when the female's abdomen hits the substrate, e. g. leaves. This sound is considerably weaker to a human ear compared to that of the male's 'calling' drumroll. Moreover, the period between pulse peaks is somewhat longer compared to that of the male. Period length (in ms) in Fig. 11: male 37.3 ± 2.0, female 47.8 ± 4.6; in Fig. 12: male 36.4 ± 2.0, female 72.3 ± 7.3. The female has no specialized hairs on the abdominal venter (fig. 9 in KRONESTEDT 1984). Moreover, there are no knob-tipped female abdominal hairs as found in species of other lycosid genera (ROVNER *et al.* 1973)[also lacking in some species of *Arctosa* (FUJII 1983)].

The sexes will perform percussive behaviour in alternation (see Figs. 11-13). Male and female drumrolls may occasionally show some overlapping and the female may, in instances, proceed with a drumroll even without the male's drumroll in between. The male will mount the female immediately following a drumming sequence of a somewhat longer duration (Fig. 10) than the usual 'calling' pulse-trains. By then, the female has lowered her cephalothorax in a receptive posture. When mounting, the male will rapidly vibrate his second leg pair.

'Duetting' is highly variable in total duration. Among the recorded 'duets', the male+female drumroll pairs varied between 2 (ended with mounting) and 26 (ended without mounting). As an example, 24 consecutive pairs of male+female drumrolls in strict alternation (including a short pause between each pair) were performed in 240 s. Towards the end of a 'duet', the female may take up a receptive posture (no drumming) but will proceed with 'replying' drumming if the male does not mount but continues to drum.

The female will respond to a drumming male with or without visual contact (as when hidden among leaves below the male).

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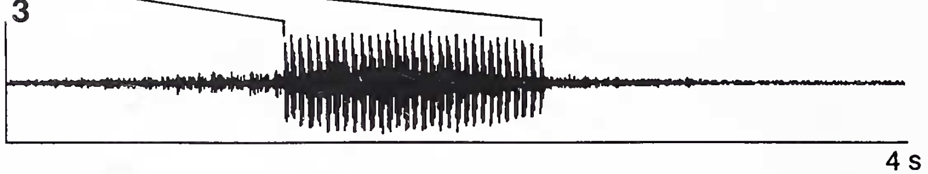

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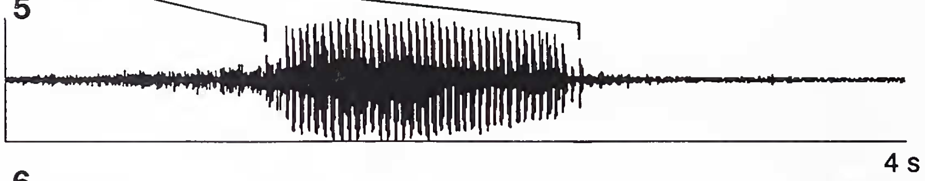

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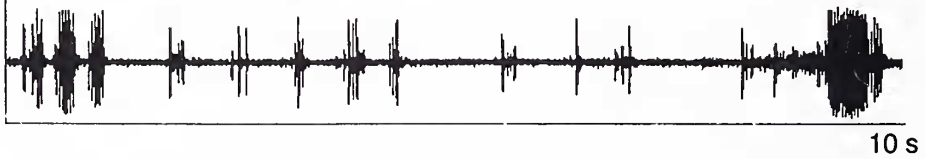

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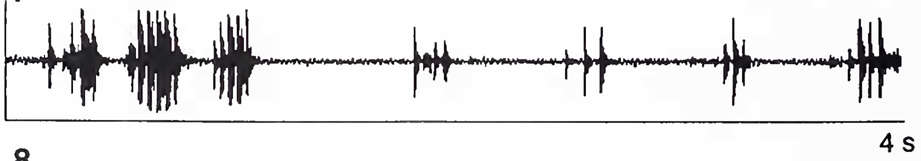

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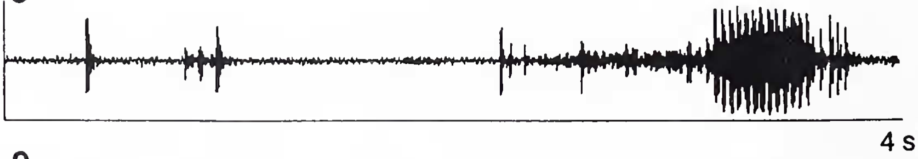

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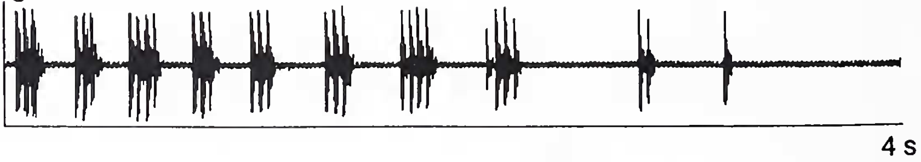
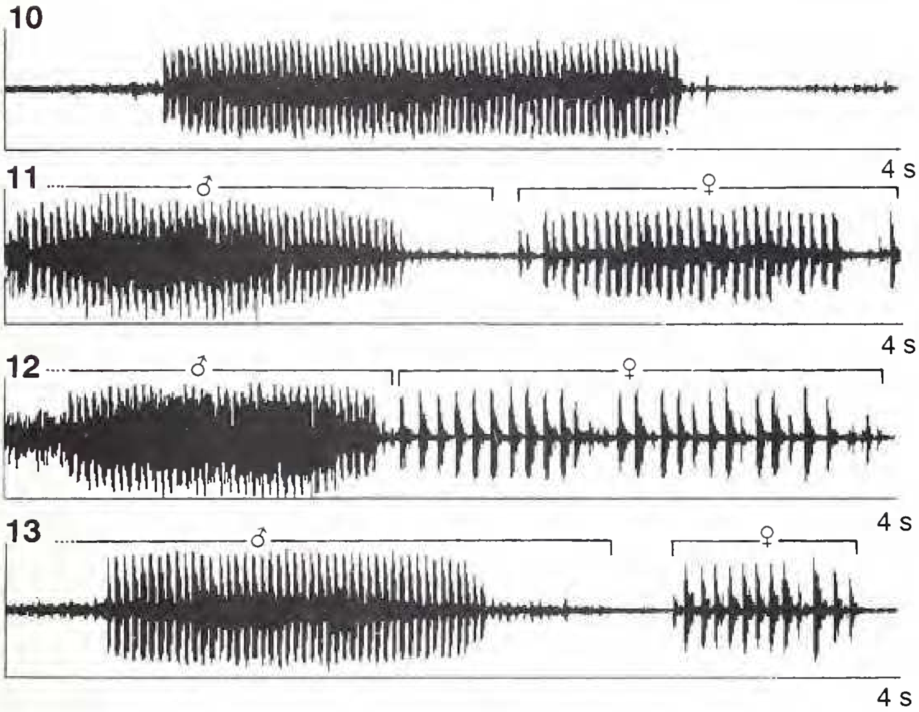




FIGS 2-13

Hygrolycosa rubrofasciata. Oscillograms of acoustic effects of percussion behaviour, on paperboard. - 2-5. 'Calling' drumrolls; 3 and 5 are details of 2 and 4 respectively; 2, 3 and 4, 5 show records from two different males respectively (in female presence). - 6-9. Agonistic percussion; 7 and 8 show details of the sequence shown in 6; 9 is a record from another male. - 10. A male's drumroll just prior to mounting a female. - 11-13. Male-female 'duetting'; different females, same male in 12 and 13.

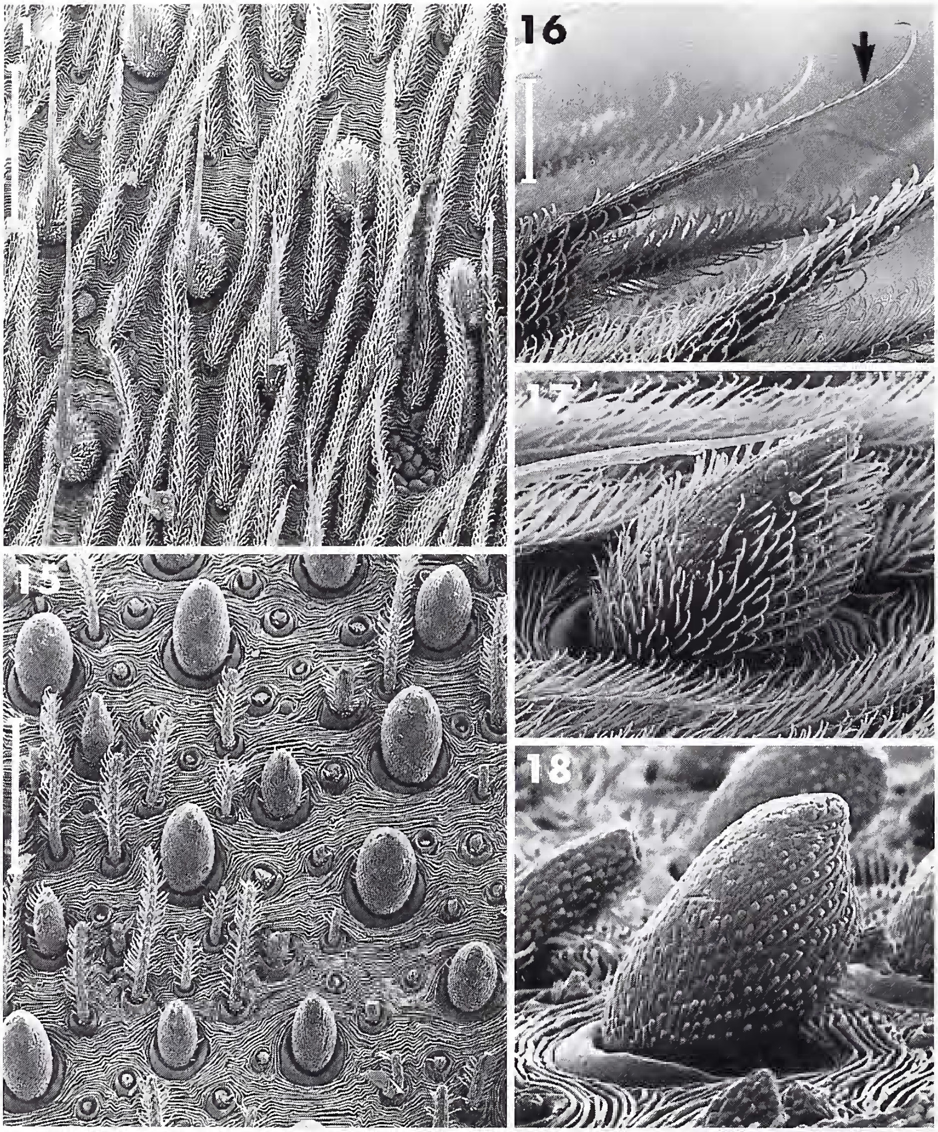
Agonistic percussion in males

During male-male encounters, one of the males may show aggressive behaviour by trying to chase the other away. The dominant male will simultaneously emit a series of brief audible percussive pulse-trains (by abdominal tapping) (Figs. 6-9) which form a certain temporal pattern. At the beginning of a series, each pulse-train is longer than later in the series (Figs. 7 & 9). The pulses in the first brief drumrolls are often louder than in the subsequent shorter ones. In many of the observed encounters, the series concluded with a longer pulse-train (Fig. 8), reminding of a short 'calling' drumroll and with similar period length between pulses.

STRUCTURAL MODIFICATIONS ASSOCIATED WITH VIBRATION PRODUCTION

Abdominal hairs

The adult male has the ventral abdominal cuticle thickened and covered with numerous knob-like hairs (Figs. 14 & 15) which apparently improve the impact

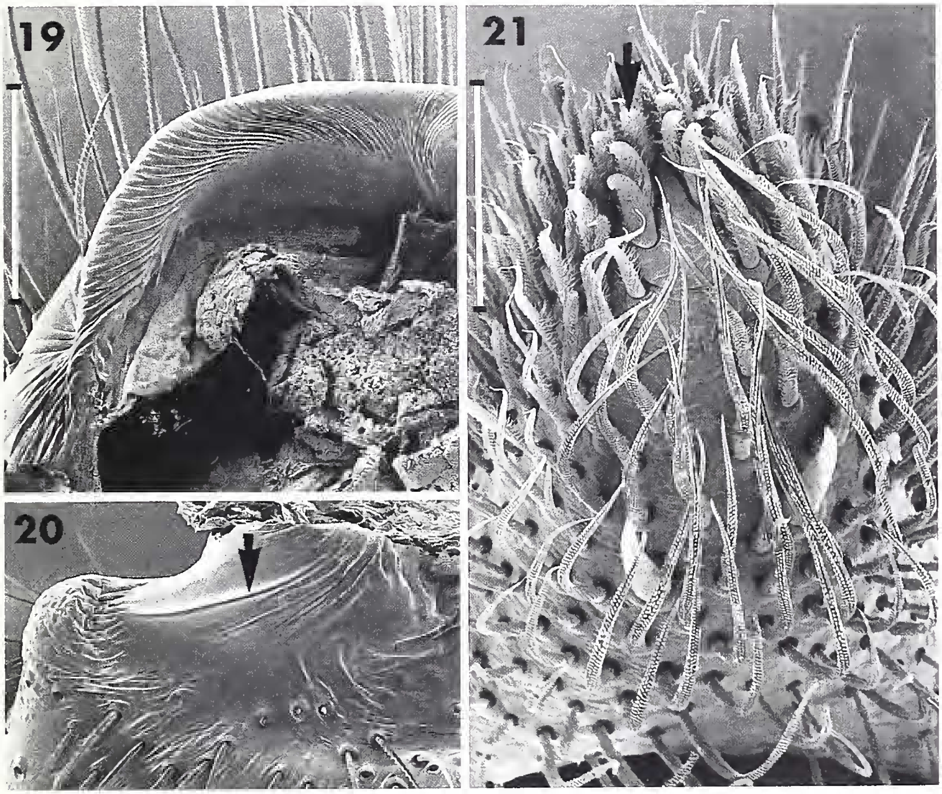


FIGS 14-18. *Hygrolycosa rubrofasciata*, adult male. - 14. Venter of abdomen of male caught early (April) during the mating period. The picture shows knob-like hairs with (to the left) and without apical portions (to the right) at some distance from the middle of the venter. At the middle, all knob-like hairs were devoid of the apical portion. - 15. The same of a male caught in mid-May. Note the worn hair-covering. The knob-like hairs lack both narrow apical portion and small hair-like filaments.- 16-18. Knob-like hairs: 16, apical portion *(arrow)* in a male apparently newly moulted to adult (caught at Turku, Finland 3 Sept. 1978); all knob-like hairs were intact. 17, from specimen caught at the end of April. 18, from specimen caught in mid-May; knob-like hairs lack both apical portion and small hair-like filaments (note the spiral arrangement of these filaments). Scale lines: 50 µm (14, 15), 10 µm (16-18, all same magnification).

during drumming. The knob-like hairs originally terminate in a narrow apical portion (Figs. 14 & 16) which is later worn off (Fig. 17). In aged males, even the numerous hair-like projections from each hair have been worn off due to repeated tapping of the abdomen against various objects (Figs. 15 & 18).

Presumed tibio-cymbial stridulatory apparatus

The palp of the adult male shows structural modifications which may act together as a stridulatory apparatus. The file consists of a regular series of grooves on the inner side of the arch-shaped dorso-distal projection of the tibia (Fig. 19) while the scraper is formed by a ridge at the base of the cymbium (Fig. 20). The cymbium is equipped with a number of short spines at the tip as well as with two longer spines and several long stout hairs on the bulging ventral side between alveolus and tip (Fig. 21). It is assumed that



Figs 19-21. *Hygrolycosa rubrofasciata*. - 19-20. Adult male, presumed stridulatory apparatus, left palp: 19, dorso-distal projection of tibia showing grooves (pars stridens) on prolaterad half of inner side; 20, dorsal aspect of cymbium base with ridge-shaped scraper (plectrum, *arrow*) on prolaterad part. - 21. Adult male, tip of left palp; note group of stout spines at the tip (*arrow* pointing at one of these spines) and the two spines between tip and alveolus. Scale lines: 100 µm (19 & 20 same magnification).

the stridulatory apparatus will produce some still not discerned substrate-coupled vibratory sensation by the oscillating movements of the palps described above. The spine armature may be involved in contacting the palpal tip to the substrate (cf. ROVNER 1975).

DISCUSSION

Different strategies for locating and recognizing a conspecific mate have evolved among lycosid spiders. Any combination of chemical, visual, tactile and/or vibratory (incl. acoustic) signalling may be involved in intersexual communication.

Precopulatory behaviour in male spiders, including various lycosids (for refs. see TIETJEN & ROVNER 1982), may be induced by pheromones associated with female draglines. In certain lycosid species, females thriving among dead leaves on the ground may build up an "odour cloud" affecting conspecific males within a short distance (*Schizocosa:* TIETJEN 1979). In *H. rubrofasciata*, however, the proximity of a female does not seem necessary for eliciting the 'calling' behaviour in the male. Dragline pheromones are most probably of little or no significance for locating females and inducing precopulatory behaviour in this species because the females are rather inactive in comparison to the males during the mating period. This can be inferred from pitfall trap data from most of this period (KRONESTEDT 1984; slightly higher activity was shown by females carrying egg sacs later in the spring, probably due to their search for suitable sites for warming the eggs in sun light). [KÖHLER & TEMBROCK (1987) were not even able to establish the presence of any females at their study site.] Whether an "odour cloud" among leaves, effective within a short distance, may be built up by female *H. rubrofasciata* is not known. Such a chemical component does not, however, seem to be of necessity in this species. Before visual contact, a receptive female will very markedly respond to a male's 'calling' behaviour by oscillating her body, producing a 'replying' drumroll. Chemical, tactile and visual cues may be of significance at short distance prior to the male mounting the female for copulation. From observations indoors, it was apparent that a male immediately recognized a female after a first brief bodily contact; a male also reacted to another male by threat behaviour after brief touching. Cuticular pheromones may be involved in recognition by touch. KRONESTEDT (1986) assumed that cuticular pores found on the legs of various lycosids may be the sites for emitting such pheromones, and JUBERTHIE-JUPEAU *et al.* (1990) showed that in at least one species (*Alopecosa cuneata*) each pore is connected with an epithelial secretory unit. Similar cuticular pores do occur on the legs in both sexes of *H. rubrofasciata* (pers. obs.)

The male-female percussive 'duetting' in *H. rubrofasciata* is sofar known unique among lycosids. Reciprocal 'duetting' has, however, been thoroughly studied in different species of the ctenid genus *Cupiennius* (ROVNER & BARTH 1981; BARTH 1993, with further refs.), nocturnal hunters associated with certain plants in Central America. In these species, the male and female vibratory signals (substrate-borne vibrations transmitted through plants) are also exchanged in alternation. The male signals are species-specific in contrast to those of the females. The sexes will locate each other by repeated reciprocal signalling.

Signalling by percussion (tapping by palps, first legs and/or abdomen) and/or stridulation is found in males of various lycosid genera (for refs. see UETZ & STRATTON 1982). Some of the species producing sounds audible to a human ear seem to depend on a certain kind of substrate for signalling. As is the case with *H. rubrofasciata*, dry leaf litter seems to be suitable for transmitting signals produced by percussion or stridulation, e. g., in *Gladicosa gulosa* (Walckenaer) (HARRISON 1969) and some different *Schizocosa* species (e. g. STRATTON 1991). In *H. rubrofasciata*, the presence of leaf litter is important for the signalling of both sexes as well as for providing a suitable three-dimensional space for the females' secluded habits.

Like in *H. rubrofasciata*, modifications of the ventral abdominal hairs may occur in other lycosid species with a ritualized abdominal tapping behaviour [e. g. *Pardosa sphagnicola* (Dahl): HOLM & KRONESTEDT 1970 and own obs.; *P. hyperborea* (Thorell): WUNDERLICH 1984 and own obs.; and *P. schenkeli* Lessert: own obs.]. The corresponding hairs differ, however, in detail from those in *H. rubrofasciata* and have apparently evolved by convergence due to behaviour. KÖHLER & TEMBROCK (1987) meant that the fully developed knob-like hairs ('Tymbalhaare') in *H. rubrofasciata* lacks 'secondary hairs' and that this is not due to wearing. As seen in Figs. 16-18, these hairs do develop with 'secondary hairs' which are later, like the apical part of the hair, worn off by repeated drumming.

The number of pulses in a 'calling' drumroll of *H. rubrofasciata* is subject to some variation between individuals, as was also noted by KÖHLER & TEMBROCK (1987). There may as well be a certain variation in the same individual which could be due to motivation. The length of an "ordinary" 'calling' drumroll has, however, been of a the same magnitude in duration (around 1 s) in this study as well as in previous records [von Helversen in WEYGOLDT (1977, fig. 8 - note: time scale needs correction): c. 750 ms; KRONESTEDT (1984, fig. 3): 1070 ms; and KÖHLER & TEMBROCK (1987, fig. 4): c. 875 ms for a drumroll consisting of 25 pulses, though they noted a variation between 17 and 41 pulses in different drumrolls]. The lengths of period between pulse peaks were roughly of a similar magnitude in duration (around 30-40 ms) in the present as well as in the previous studies.

The indistinct sound preceding a 'calling' drumroll may be attributed to palpal movements and/or oscillations of some other body parts (e. g. abdominal oscillations without the venter hitting the substrate) though this is not fully clear. The rattling sound following at the end of such a drumroll may have a similar explanation. Future studies with refined techniques may throw more light on this.

The humming sound heard just prior to a 'calling' drumroll is somewhat enigmatic. It could perhaps be of the same kind as that described by ROVNER (1980) as "analogous to the generation of flight-sounds in insects", i. e., produced by some vibrations of abdomen or appendages. As suggested by ROVNER (1980, p. 199) such a humming sound will be masked by the louder output due to percussion (here: abdominal drumming) or stridulation.

Agonistic behaviour involving vibratory signalling has been studied only in a few lycosid species (Rovner 1967, Fernandez-Montraveta & Schmitt 1994). In *H. rubrofasciata*, the agonistic drumming consists of repeated brief pulse-trains, in comparison with the longer pulse-trains in the 'calling' or courtship drumrolls. Analogous difference between agonistic and courtship behaviour was found in *Rabidosa rabida* (Walckenaer) (Rovner 1967) in which the sound-producing behaviour during threat display resulted in a number of brief bursts of pulses (elicited by palpal movements) compared with pulse-trains of longer duration during courtship display. *H. rubrofasciata* and *R. rabida* both showed a considerable variation in the agonistic signals as concerns the number of pulses in each brief pulse-train as well as in the time interval between pulse-trains.

The presence of a presumed stridulatory apparatus in male *H. rubrofasciata* may be compared with a probably homoplastic arrangement found in species of the genera *Hogna* (at least some Nearctic species referred to this genus), *Gladicosa*, *Rabidosa*, and *Schizocosa* (Rovner 1975). Species in these genera are also provided with a stridulatory apparatus located at the tibio-cymbial joint but the grooves on the inner side of the dorso-distal arch-shaped projection are more transverse and the scraper at the base of the cymbium differently shaped compared with the condition in *H. rubrofasciata*. When differing in details, a corresponding location of a stridulatory apparatus in phylogenetically not too distant species does not necessarily imply that the conditions are homologous (cf. Starck 1985). A tibio-cymbial configuration similar to that in *H. rubrofasciata* was, however, detected in *H. umidicola* (own obs.). A resemblance in the distal spine equipment on the cymbium between the two species was also found. These similarities are indubitably homologous as regards the two *Hygrolycosa* species (in contrast to *H. rubrofasciata*, male *H. umidicola* lacks abdominal knob-like hairs).

The mechanical signalling in *H. rubrofasciata* certainly deserves further analyses from different aspects, e. g., "dissection" of vibration output (especially substrate-borne vibrations), dependence of male ‘calling’ behaviour on temperature, on female presence, &c.

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